Calanus in North Norwegian fjords and in the Barents Sea

KURT S. TANDE

K. S. Tande. 1989: *Calanus* in North Norwegian fjords and in the Barents Sea. Pp. 389–407 in Sakshaug, E., Hopkins, C. C. E. & Øritsland, N. A. (eds.): Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990. *Polar Research 10(2).*

The physical environment of a North Norwegian fjord and of the Atlantic and Arctic domains of the Barents Sea are described. The seasonal variation of primary production and biomass of the most important copepod species are described in order to contrast regional differences in the timing of the plankton cycles. Analysis of the seasonal variation in the biomass of six different copepod species in Balsfjorden clearly demonstrate the importance of *Calanus finmarchicus* as a spring and early summer form, whereas *Pseudocalanus acuspes*, the most important smaller form, reaches the highest biomass later during the productive season. In the Atlantic part of the Barents Sea, *C. finmarchicus* is the dominant herbivorous form. The next most important species, *Pseudocalanus* sp. and *M. longa*, play a less important role here than in Balsfjorden. In the Arctic domain, the smaller copepod forms appear to have been replaced in trophodynamic terms by the youngest year-group (C-CIII) of *C. glacialis*, which prevails during the Arctic summer and autumn periods. The coupling between primary producers and *Calanus* on a seasonal basis is addressed through the grazing and the vertical organisation of the plant-herbivore community. The productivity of these two *Calanus* species is considered in relation to the seasonal and inter-annual variation in climate; although different mechanisms are utilised, cold periods tend to lower *Calanus* productivity both in the Arctic and the Atlantic domains of the Barents Sea. Interannual variations in *Calanus* biomass and productivity are discussed in the perspective of endemic and advective processes.

Kurt S. Tande, Department of Aquatic Biology, Norwegian College of Fishery Science, University of Tromsø, N-9001 Tromsø, Norway

Introduction

The ecology of the North Atlantic has been intensively studied for several decades. The majority of the studies have concentrated on the eastern region, with most effort probably concentrated on the North Sea, the Norwegian Sea, and the adjacent continental shelf. The Norwegian Atlantic current transports Atlantic Water northeastwards, thereby creating a marine environmental continuum which extends to the Barents Sea and further northwards to the western coast of Svalbard (Blindheim & Loeng 1981). With these fairly homogeneous physical environmental conditions we would expect to find a plankton community which is structured and functions basically in the same way throughout the entire area. In this study the physical environments of a North Norwegian fjord and the Atlantic and Arctic domains in the Barents Sea are described. The seasonal variation of primary production and biomass of the most important copepod species are also described in order to contrast any regional differences in the timing of the plankton cycles. Species succession in the phytoplankton and copepod communities is described in order to characterise differences among the pelagic communities from neritic coastal waters in northern Norway, the Atlantic waters of the Barents Sea, and the Arctic portion of the Barents Sea.

The species composition and seasonal growth cycles of herbivorous copepods have been described in the Norwegian fjords by Hopkins et al. (1984, 1985). The most abundant herbivorous copepod species belong to the genus *Calanus*, and *Calanus finmarchicus* should be considered the key species throughout the area of Atlantic waters (Matthews 1967; Jaschnov 1970, 1972). The geographical range of *C. hyperboreus* and *C. glacialis* is related to different water masses which link the former to deep water masses in the Norwegian Sea and to Arctic waters in the Northern Hemisphere (Jaschnov 1967). The only true Arctic species, *C. glacialis*, is consistently present in waters north of the Polar Front. This paper presents data for seasonal biomass cycles of the most important copepods in the region, with special

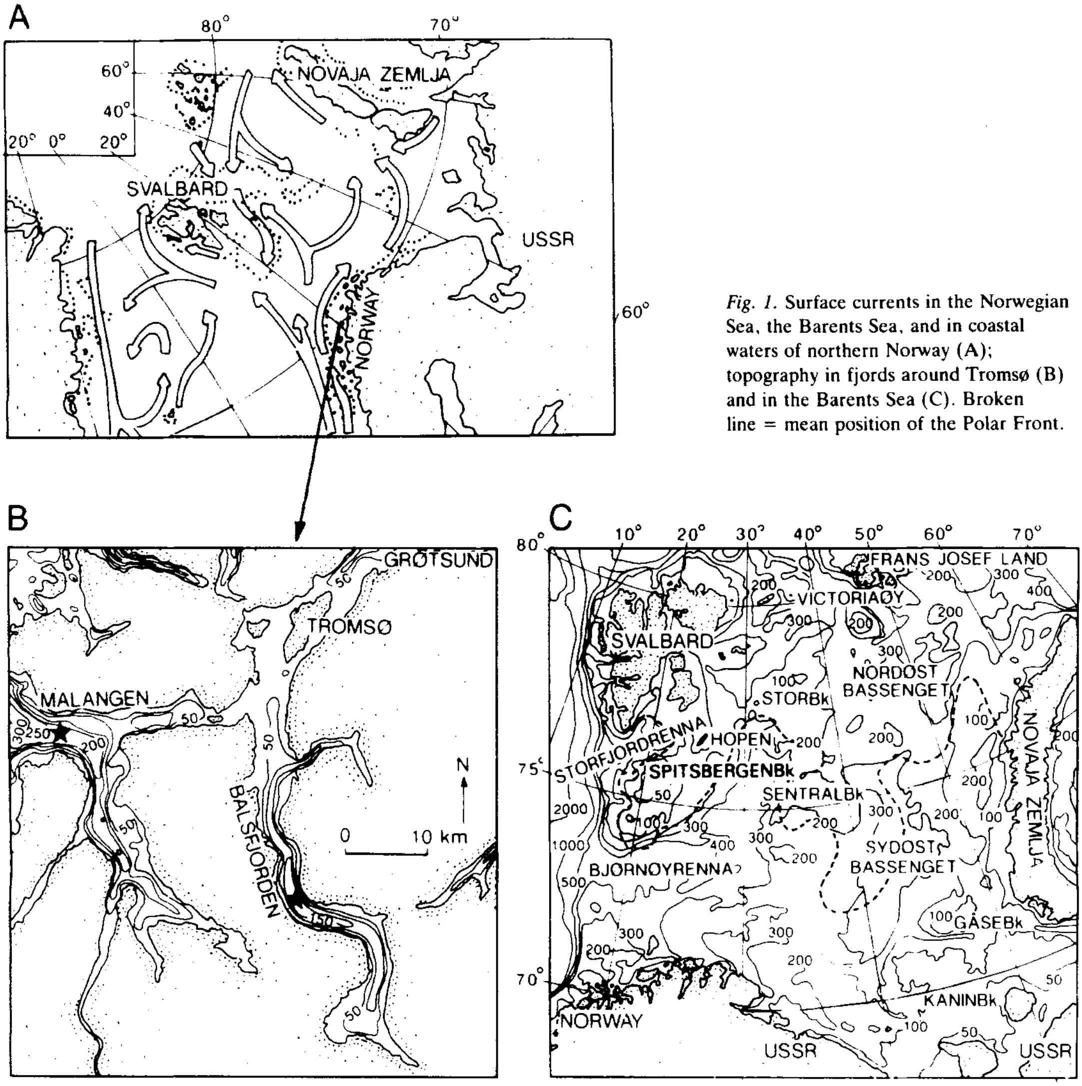

Fig. 1. Surface currents in the Norwegian Sea, the Barents Sea, and in coastal waters of northern Norway (A); topography in fjords around Tromsø (B) and in the Barents Sea (C). Broken line = mean position of the Polar Front.

emphasis on *C. finmarchicus* and *C. glacialis* in the Barents Sea ecosystem. Climatic changes could modify the productivity of these two species. I attempt to explain the biological basis behind such a possible modification. The trophodynamic role of *Calanus* and the vertical organisation of the plant-herbivore relationship are discussed, based on data obtained mainly during the Pro Mare programme.

The physical environment

The seasonal and interannual variations in the physical environment in coastal waters of northern Norway and in the Barents Sea are to a large extent driven by processes in the oceanic North Atlantic (Cushing & Dixon 1976). The North Atlantic Current enters the Norwegian Sea mainly through the Faroe-Shetland Channel. Before it reaches the Norwegian continental shelf between 62 and 63°N, a branch diverts into the North Sea along the western and southern slopes of the Norwegian Channel (Blindheim & Loeng 1981). The bulk of the Atlantic Water flows northwards and splits in two branches off the coast of Troms, in northern Norway. One branch continues northwards as the West Spitsbergen Current, and the other is diverted into the Barents Sea as the North Cape Current.

North Norwegian fjords

The Atlantic Water is, to a certain extent, isolated from the coast of Norway by the Norwegian Coastal Current. Freshwater from the Baltic Current mixes with North Sea and Atlantic waters to form the northward flowing Norwegian Coastal Current. Light coastal water spreads out in a wedge form above the heavier Atlantic Water. The seaward extent of this wedge of coastal water varies seasonally and reaches its maximum in winter. Along the Norwegian coast there is a further supply of freshwater runoff, but in spite of this there is an increase in salinity towards the north which is due to mixing with Atlantic Water.

Although Balsfjorden (69°N; 19°E) is generally a cold fjord, the physical environment is considered to be representative of North Norwegian fjords (Fig. 1). The general topography, seasonal temperature variation, salinity, and stability are described in Eilertsen et al. (1981). These fjords have from one to several basins with a maximum depth of ca. 200 m. The temperature varies from about 1 to 7°C, and the salinity ranges from ca. 32.80 to 34.00 during most of the year.

Barents Sea

The Coastal Current enters the southeastern region of the Barents Sea. The southern part of the Atlantic Current continues eastward together with the Norwegian Coastal Current and proceeds along the Murman coast as the Murman Current (Midttun & Loeng 1987). A northern part (North Cape Current) transports Atlantic Water into the Barents Sea along the channel, Bjørnøyrenna. The influx of Arctic Water to the Barents Sea takes place along two main openings between Frans Josef Land and Novaja Zemlja (Dickson et al. 1970). The area where the Atlantic and the Arctic water masses meet is called the Polar Front. In the area west of Sentralbanken, the Polar Front is sharp and shows features typical of the bottom topography. In the eastern Barents Sea, the frontal area is less distinct, and mixed water masses cover large areas (c.f. Fig. 1).

Atlantic water masses are, in general, defined by salinities of >35.00 (Helland-Hansen & Nansen 1909). At the entrance to the Barents Sea, the mean salinity and temperature in the core during the period 1967–1977 were 35.13 and 6.2°C, respectively (Blindheim & Loeng 1981). Further east, the characteristic change to lower salinity and temperature has been demonstrated by Loeng & Midttun (1984). Arctic Water, or the Barents Sea Winter Water, is mainly found in the intermediate layer (from 20 to 150 m) in the northern Barents Sea. The core is usually found between depths of 30–60 m with a temperature below −1.5°C and a salinity between 34.4 and 34.6 (Midttun & Loeng 1987).

Seasonal variations in the position of the ice border are, in general, similar from year to year with maximum and minimum extension in March-May and August-September (Loeng & Vinje 1979). Ice formation usually starts in late September or October, and the ice border moves rapidly southwards to the Polar Front during November and December. The retreat of the ice starts in May. In the beginning, the rate of melting is slow, but it increases and reaches its maximum in July and early August. Considerable interannual variations in sea ice extension occur and variations within the extremes can exceed 500 km, especially in summer and autumn. Large variations in the temperature of the Atlantic waters have been observed which indicate variability in the inflow and/or cooling of these water masses (Ådlandsvik 1989). A more comprehensive description of the physical environment in the Barents sea is given in Loeng (1991 this volume).

The biological environment

Primary production

In Balsfjorden, in northern Norway, the light regime varies considerably on a seasonal basis, with negligible or immeasurable light in December and January (Eilertsen & Taasen 1984). The sun stays below the horizon from 26 November until 18 January and is continuously above the horizon during the period of midnight sun from 28 May to 19 July. At the end of March mean daily radiation is more than 200 ly d^{-1} until the end of August. The primary production period starts in March, reaching a maximum of ca. 650 mg C d^{-1} in mid-April, followed by a culmination period in May (Eilertsen & Taasen 1984). A subsidiary peak in production, although not necessarily a yearly phenomenon, occurs during August and September through stability deformation in surface waters (Eilertsen 1983; Eilertsen & Taasen 1984). Integrated annual primary production for the years 1976–1978 is ca. 120 g C m^{-2}.

In the Barents Sea, physical conditions may be very different from one area to another, mainly because ice tends to reduce atmospheric influences on the water masses. Additional variability is enforced by bottom topography, currents, and differences in the physical conditions of the seawater. Spring phytoplankton blooms are the result of light intensity at a particular depth and the rate of vertical mixing of the water column. Water column stabilisation is necessary for the onset and development of any high latitude spring bloom (Sverdrup 1953; Sambrotto et al. 1986).

Two different sets of conditions, although not mandatory for the onset of the spring bloom, could exist during spring in the Barents Sea. First, when the ice extends to the south of the Polar Front, Atlantic Water could initiate the melting of ice early in the spring, due to its relatively high water temperatures. This would, in principle, have the same effect as the melting period due to increased solar radiation which would normally take place at a later period in true Arctic Water. Such melting enhances stability, and favours an intense spring phytoplankton bloom (see Fig. 7). Second, the oceanic waters not influenced by ice formation are most frequently found in the Atlantic domain. The yearly build-up of the thermocline in these waters takes place in June, generally with low stability of the water masses throughout April and May (Skjoldal et al. 1987). This would tend to shift the culmination of the phytoplankton bloom towards the end of May and the beginning of June, although a substantial primary production has taken place during April and May. Using model simulations, the annual primary production has been estimated to be ca. 70 g C m^{-2} yr^{-1} and 55 g C m^{-2} yr^{-1} in the Atlantic and Arctic domains, respectively (Slagstad & Tande 1990; Tande & Slagstad 1991)

Information from field investigations in the Barents Sea indicates that the spring phytoplankton bloom is initiated in April in unstratified Atlantic water masses (Skjoldal et al. 1987; Eilertsen et al. 1989). In the fjords of the western coast of Svalbard, at a latitude of 8–10° further north, the spring bloom was shown to start at approximately the same time as the spring bloom in the coastal areas of northern Norway (Eilertsen et al. 1989). It is noteworthy that the spring bloom in the Balsfjorden area and in the Atlantic Water of the Barents Sea occurs in unstratified water masses. This means that the rate of vertical mixing in these areas allows for net phytoplankton production before any of the conventional physical criteria show any density gradient. Eilertsen et al. (1989) draw attention to the fact that after the vernal equinox (21 March) the day-length increases at a faster rate at high latitudes, and that this rapid increase in day-length enhances primary production when compared to areas further south. They conclude that the critical depth is deeper in northern areas, since the days are longer further north and the global radiation values are comparable between, for instance, 70 and 78°N from March to May. Thus, stratification of the water masses in the Barents Sea tends to fix the time of culmination rather than the onset of the spring phytoplankton bloom in the Atlantic Water of the Barents Sea.

Composition of phytoplankton species

In fjord areas in northern Norway flagellates of size <5 μm prevail regularly during the pre-bloom period in March (Eilertsen pers. commun.), whereas the diatoms *Chaetoceros socialis, Nitzschia grunowii, Thalassiosira gravida/rotula, T. nordenskioeldii*, and the prymnesiophyte, *Phaeocystis pouchetii*, constituted the bloom in April and May. The proportion of diatoms and *P. pouchetii* in the phytoplankton during the spring bloom shows a shift toward a predominance of *P. pouchetii* during May and June (Eilertsen et al. 1981; Eilertsen & Taasen 1984). During the autumn, small amounts of *P. pouchetii* were present together with the coccolithophorides *Anthosphera robusta* and *Emiliania huxley*, as well as small amounts of diatoms and dinoflagellates.

Data from Trondheimsfjorden (63°N) in the south to Ullsfjorden (69°) in the north show that the species *Chaeotoceros socialis, Phaeocystis pouchetii*, and *Skeletonema costatum* are common components of the spring phytoplankton in five different localities along the coast (Gaarder 1938; Sakshaug 1972; Heimdal 1974; Schei 1974; Eilertsen et al. 1981). Eilertsen et al. (1981) attribute this similarity among the dominant species to the estuarine circulation which prevails between the fjords and the Norwegian Coastal Current.

A correspondingly detailed description of the seasonal succession in phytoplankton species composition in the Atlantic and Arctic waters of the Barents Sea is unavailable. Nevertheless, diatoms of the genera *Chaetoceros*, *Thalassiosira*, and *Nitzschia*, and the prymnesiophyte *Phaeoecystis pouchetii*, are the most important species in these waters. The species succession during the spring and early summer period tend to show the same pattern as found in coastal waters in northern Norway (Eilertsen pers. comm.). Blooms associated with the ice edge tend to be characterised by slightly different floral assemblages, both in Atlantic and Arctic waters. The under-ice phytoplankton species *Melosira arctica*, *Thalassiosira bioculata*, and *Actinocyclus* sp. prevail in multi- and two-year-old ice, whereas the pennate diatoms *Navicula vanhoeffeni* and *Nitzchia frigida* are found primarily under one-year-old ice (Nøst-Hegseth, pers. commun.). Although blooms of these species are associated with the under ice surface, *Thalassiosira* spp. can be found as important members during the spring bloom in pelagic waters during the retreat of the ice edge.

Regional differences in the copepod community

In Balsfjorden, in northern Norway, the total copepod biomass in 1977 was in general low during winter and spring, and the maximum appeared late in the summer (Fig. 2). Compared to more oceanic environments, for example the ocean weather station I (OSW I) in the North Atlantic, a two-fold higher annual primary production in Balsfjorden translates into higher overall standing stocks of copepods, with mean monthly averages of 24 mg wet weight m^{-3} at OSW I (Parsons & Lalli 1988, fig. 7) and 18 mg dry weight m^{-3} in Balsfjorden (Fig. 2). Primary production and copepod production, reflected in biomass build-up, appears to be more closely coupled in the North Atlantic than in Balsfjorden. Peaks in phytoplankton production and zooplankton biomass at OSW I were in June, while in Balsfjorden the peaks were in April and in the autumn. This is, in general, considered to be a combined effect of differences in temperature, species composition, and life cycle patterns of the species involved in these two environments.

Detailed descriptions of the zooplankton community in Balsfjorden, based on data obtained during the second half of the 1970s, have been given by Tande (1982) and Hopkins et al. (1984). Six different copepod species occur regularly throughout the year in this fjord (Fig. 3). Among the smaller forms are the calanoid *Microcalanus pusillus* and the cyclopoid *Oithona similis*. Species of intermediate size (adult size < 1.5 mm in prosome length) are *Acartia longiremis* and *Pseudocalanus acuspes*. *Metridia longa* and *Calanus finmarchicus* are the larger copepods in the fjord. Occasionally, *C. hyperboreus*, *Temora longicornis*, and *Euchaeta norvegica* are recorded in the fjord and are possibly associated with the inflow of oceanic waters in the coastal current. Population data were obtained from Balsfjorden for *M. longa* via sampling once or twice a month during 1978 (Grønvik & Hopkins 1984) and monthly for all the other species during 1977.

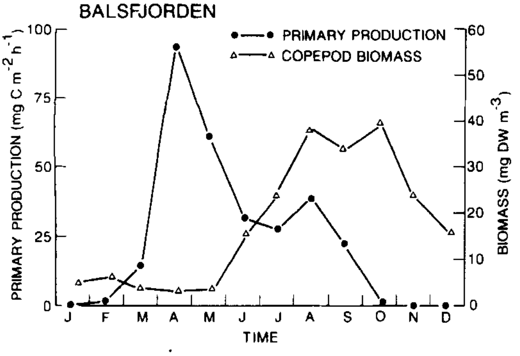

Fig. 2. Seasonal variation in primary production and copepod biomass in Balsfjorden, northern Norway, in 1977. The primary production data are adopted from Eilertsen & Taasen (1984).

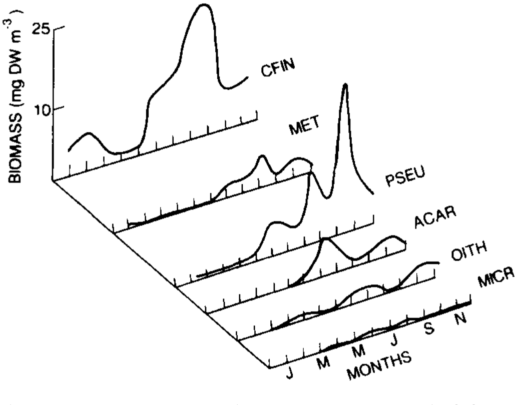

Fig. 3. Seasonal variation in biomass for the copepods *Calanus finmarchicus* (CFIN), *Metridia longa* (MET), *Pseudocalanus acuspes* (PSEU), *Acartia longeremis* (ACAR), *Oithona similis* (OITH), and *Microcalanus pusillus* (MICR) in Balsfjorden.

Copepod biomass

Calculations of the biomass are based on dry weight data from various sources. Adult dry weights of *Microcalanus pusillus* of 5.7 µg and a mean dry weight of 1.6 µg for CI-CV are calculated from data given in Davis (1984), assuming 40% of the dry weight as carbon content. The cyclopoid copepod *Oithona similis* is converted to biomass by assuming a mean dry weight of 1 µg (CIV) and 2.2 µg for copepodite stages and adults, respectively. Data for adults are given by Evans (1977), and the dry weight for CIV is calculated assuming a 50% weight increment per stage (see McLaren et al. 1989). Adult dry weights of 6 µg have been obtained for *Acartia longiremis* from waters around Tromsø (Norrbin et al. 1990). Carbon contents for copepodite stages are given by Berggreen et al. (1988) and have been converted to dry weights assuming a dry weight carbon content of 40%. Taking a dry weight of 10 µg for CV and adult *Pseudocalanus acuspes* (Norrbin et al. 1990), dry weights for the other copepodite stages were calculated using a weight increment of 50% per stage (see Davis 1984; Klein Breteler et al. 1982). The seasonal variation in dry weights and CIV, CV, and adult *Calanus finmarchicus*, and of CV and adult *Metridia longa* are given in Tande (1982) and Grønvik & Hopkins (1984). For CI-CIII *C. finmarchicus*, dry weights obtained in the Barents Sea were adopted in the present calculation (Tande & Slagstad 1991). For copepodite Stages I-IV of *M. longa*, the dry weights have been calculated by converting the dry weights from corresponding stages of *C. finmarchicus* using a dry weight factor (0.4) between CV and adult females obtained from these two species in Balsfjorden (Tande 1982).

Minimum standing stocks in terms of dry weight were found during the winter for all of the species listed. The most dramatic changes were found in *Acartia longiremis*, which was virtually absent during the overwintering period (Fig. 3). A dramatic decline in *C. finmarchicus* stock is associated with the period of reproduction in March and April. The two more herbivorous species, *C. finmarchicus* and *P. acuspes*, rely to a greater extent on wax esters during the winter period (Norrbin et al. 1990) and commence spawning at the beginning of the spring bloom at the end of March (Diel & Tande 1991). The more omnivorous copepod species, *Metridia longa*, for which the intake of energy is essential during the winter season, spawns at the end of the spring bloom in May (Tande & Grønvik 1983), whereas the increase in the biomass of *A. longiremis* in May and June is probably due more to the hatching of resting eggs produced the year before (Pertzova 1974; Lindley 1990).

Clearly *C. finmarchicus* dominates during spring and early summer, whereas the smaller form, *P. acuspes*, reaches the highest biomass later in the productive season (Fig. 3). Although the variation in the biomass during the season could be partly due to advection into the fjord, the general picture of a separation in time between these two species is expected according to the generation pattern. The annual generation of *C. finmarchicus* produced from April to June shows an increase in production at the subsidiary peak in primary production during August and September which is usually found in these waters (Tande 1982). *P. acuspes* is represented by two or possibly three generations in this fjord (Norrbin 1987), giving rise to a build up in biomass in late summer and autumn (Fig. 3).

A corresponding list of copepod species can be constructed for both the Atlantic and the Arctic domains in the Barents Sea. Based on abundances

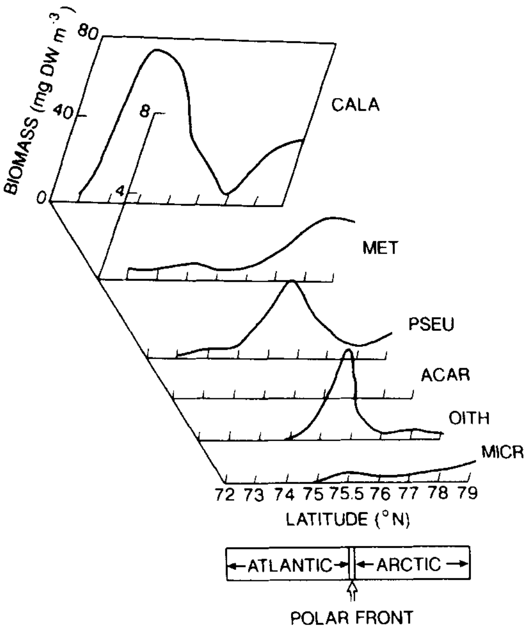

Fig. 4. Regional variations in biomass of the most quantitative important copepods during the summer and autumn of 1981 in the Barents Sea. Symbols as in Fig. 3. Redrawn from Hassel (1986).

published by Hassel (1986), biomasses have been calculated for the numerically most important copepods in the Arctic and Atlantic domains during the summer of 1981 (Fig. 4). Data were selected from two cruises on a transect covering 73°00′N to 75°59′N and 75°30′N to 78°50′N, from 27–28 June and 8–10 August, respectively (see Fig. 1). An abundance of data was converted to biomass data using the same stage-specific dry weights given above. The abundance of *Calanus* was not separated at the species level in the investigation, but Hassel (1986) found that the majority of *Calanus* spp. to the north of the Polar Front belonged to *C. glacialis*, whereas *C. finmarchicus* prevailed in Atlantic waters. In order to emphasise the differences in the copepod community across the Polar Front, the abundance of *Calanus* spp. given in June and August 1981 has consequently been converted to biomass data. This was done by adopting dry weights of *C. finmarchicus* and *C. glacialis* for the cruises in June and August, respectively. At 76°N where the two lags overlapped, the biomass of *Calanus* is given as the sum of the biomass calculated in June as *C. finmarchicus* and in August as *C. glacialis.* Dry weights for *C. glacialis* (copepodite stages and adults) and for *C. finmarchicus* are based on data from Slagstad & Tande (1990) and Tande & Slagstad (1991), respectively.

The largest copepodite stages and adults of *C. glacialis* were not quantitatively sampled by a 36-cm diameter Juday net with 180 μm mesh. Nevertheless, the overall changes in the proportion of the biomass between the species mirrors important differences in the copepod community across the Polar Front in the Barents Sea. Compared to Balsfjorden, however, there are definite changes in the proportions and the potential quantitative importance among the species. In general terms, *C. finmarchicus* appears to have attained a more central position in Atlantic waters than in the coastal areas in northern Norway, with biomasses of ca. 70 mg dw m^{-3} at 73°N in June. A reduced quantitative importance of the smaller copepod forms is also apparent, especially in the Arctic Water. The biomass of the Arctic species *C. glacialis* increases at increasing distances from the Polar Front, attaining a maximum of ca. 30 mg dw m^{-3} at 79°N. From the current data these two *Calanus* species appear in low biomasses in the region of the Polar Front, but further data analysis and investigations are required to substantiate this pattern.

The transect in August coincides with the end of the productive period, both in the most northernmost areas in the Atlantic domain and in true Arctic Water at 79°N. The more neritic species, such as *Acartia longiremis*, are recorded only occasionally in the Barents Sea (Norrbin pers. commun.) and are of minor quantitative importance. The other copepod species, *Microcalanus pusillus, Oithona similis, Pseudocalanus* spp. and *Metridia longa*, are found in lower biomasses in the Barents Sea as compared to Balsfjorden during the autumn. The two latter forms are listed as the most abundant copepods next to *Calanus* in the Barents Sea (Skjoldal et al. 1987), but the data from 1981 indicate that both *Pseudocalanus* spp. and *M. longa* play a less important trophodynamic role in the Barents Sea ecosystem compared to Balsfjorden. The biomass data show a maximum of *Pseudocalanus* spp. and *O. similis* in the Polar Front region, reflecting the annual build-up of these populations in Atlantic waters analogous to that found in Balsfjorden during the autumn. A large abundance of CI-CIII shows that *M. longa* would also have an equivalent potential (Hassel 1986), but this is not seen in the biomass build-up which is anticipated to take place later in the autumn when CIV, CV, and adults appear in the population (see Tande & Grønvik 1983). The smallest copepod species, *M. pusillus*, increases in biomass at increasing distance to the north of the Polar Front. Although biomass values are low, the species should be considered important in trophodynamic terms due to its numerical dominance in the Arctic waters of the Barents Sea.

Calanus: species distribution in the Barents Sea

The three species in the genus *Calanus* occur regularly in the Barents Sea. Although *C. finmarchicus* is considered to be Atlantic, it generally occurs near the Polar Front (Fig. 5). Depth-integrated biomasses (0–100 m) of adult female *C. finmarchicus* and *C. glacialis* given as means from four different stations obtained during a cruise with R. V. ANDENES 19 and 20 April 1986 in the same region revealed that the standing stock of adults was 132 and 96 mg C m^{-2}, respectively. Maturity analyses (unpubl. data) confirm that both species had already started spawning in this region as early as mid-April. This is consistent

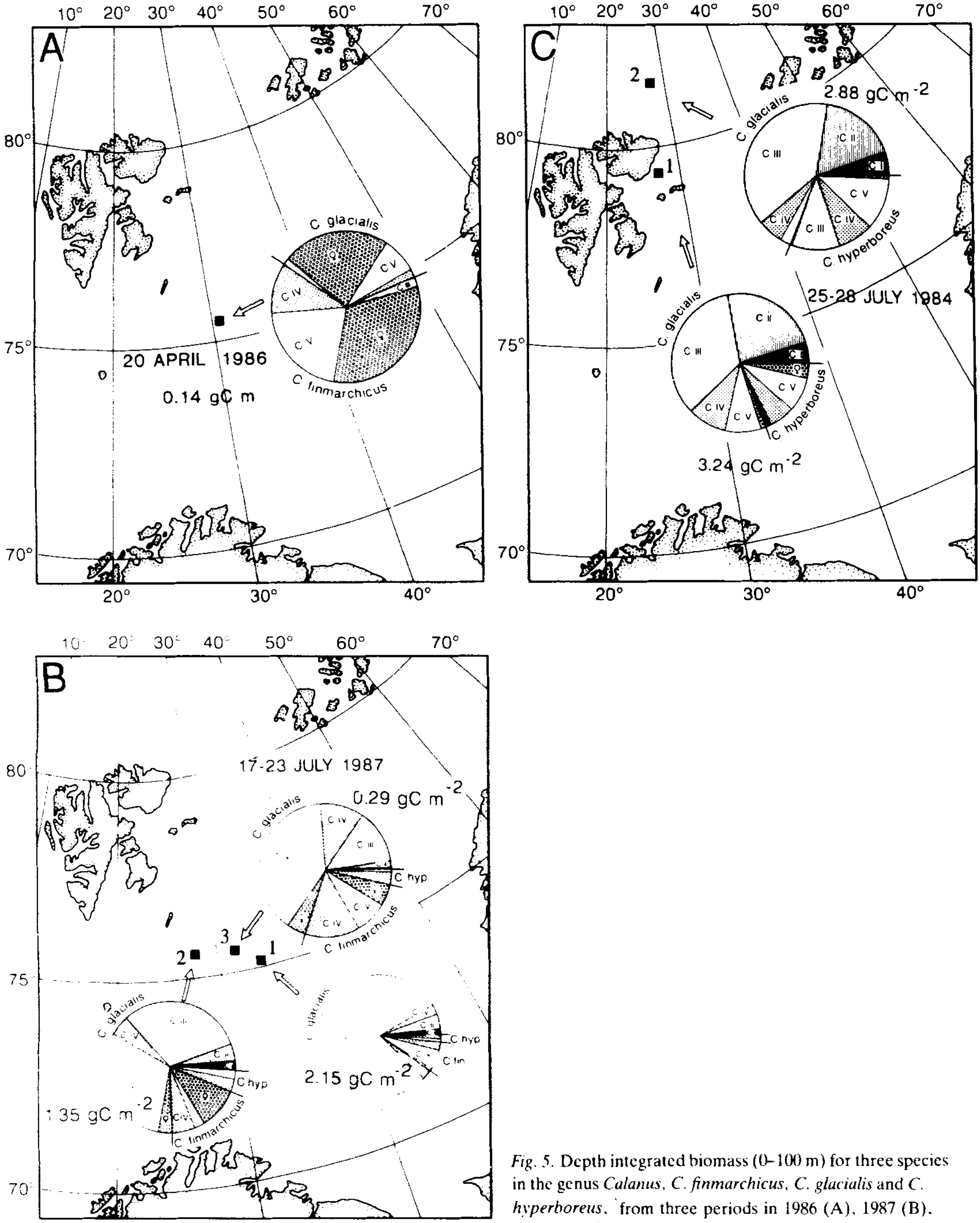

Fig. 5. Depth integrated biomass (0–100 m) for three species in the genus *Calanus*, *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, from three periods in 1986 (A), 1987 (B), and 1984 (C).

with observations for *C. glacialis* from the Fram Strait which showed pre bloom spawning at chlorophyll concentrations <0.1 mg m^{-3} at the end of March (Smith 1990).

In July 1987, although the CIV and CV dominated the biomass (Fig. 5B), CI-CIII was clearly the most abundant stages (see Hansen et al. 1990). Using depth-integrated carbon from the surface to 100 m, the biomass data were calculated from abundance data and stage specific carbon content for *C. hyperboreus*, *C. finmarchicus* and *C. glacialis* as given in Hansen et al. (1990), Slagstad & Tande (1990), and Tande & Slagstad (1991), respectively. The size frequency distributions of the CI-CIII copepodites did not show any clear species separation (see also Hansen et al. 1990, fig. 2). However, in *C. glacialis* CIV-adults prevailed both in abundance and biomass at Stations 1 and 3, while *C. finmarchicus* was found with the highest biomass at Station 2. At this time, *C. hyperboreus* was present as CIV, CV, and adult females at biomass <75 mg C m^{-2} in these waters.

In Arctic waters at 77 and 82°N (Fig. 5C), *C. glacialis* prevailed, supporting the idea that this is a true Arctic species (Jaschnov 1972; Tande et al. 1985). Depth-integrated biomass from depths of 20 to 80 m have been obtained from an investigation conducted on 25 July (Station 1) and 27–28 July (Station 2) by R. V. LANCE in 1984. The investigation is described in detail in Eilertsen et al. (1989). Due to high abundances of CI-CIII at both stations, the biomass of these stages exceeded the sum of the other copepodite stages and adults. Although CI-CIII were present for *C. hyperboreus*, the majority of biomass in this species was found as CIV, CV, and adult females. At Stations 1 and 2 this species was found with biomasses of 764 and 1297 mg C m^{-2}, respectively, which are probably underestimates but substantially above the values described for the Polar Front (Fig. 5A and B).

The data indicate that the importance of *C. hyperboreus* in terms of biomass appears to increase with latitude in the Barents Sea, at least in certain years and regions. Data from the Fram Strait indicate also that the species is found at higher biomasses in Arctic Water than in Atlantic Water (Barthel 1988; Diel 1989). This has, among other things, led to the theory that this species is Arctic (Conover 1988). However, the high biomasses generally found in the Arctic could equally well reflect low predation rates and hence increased longevity as compared to the Atlantic. The species is widely distributed and commonly found, although not reproducing, on the western coast of Norway (Matthews et al. 1978). This emphasises that *C. hyperboreus* is the most cosmopolitan of the three species in the *Calanus* complex, with an Atlantic population base dependent on deep waters for maintaining a successful life cycle.

The other two species of *Calanus* occupy the two different domains in the Barents Sea which coexist in the Polar Front region. The interchange of these two species north of the Polar Front depends on the rate of exchange of Atlantic and Arctic waters and on the balance between recruitment and mortality in the two populations. From what has been outlined above, I will in the following describe how *C. finmarchicus* and *C. glacialis* function in trophodynamic terms in the Atlantic and Arctic regions, respectively. The objective will be to delineate how climatic changes in the region could alter the potential productivity of these two species and thereby influence the rate of energy flow within the pelagic food web in the Barents Sea.

Calanus glacialis

Generation pattern and biomass

Although a two year generation cycle has been suggested for *Calanus glacialis* in the Barents Sea (Prygunkova 1968; Naumenko 1979; Tande et al. 1985; Slagstad & Tande 1990), an annual life cycle has been suggested for populations off southwestern Nova Scotia (Runge et al. 1986), for the inner Godthåb fjord (MacLellan 1967), Fram Strait (Smith 1990), and for the Davis Strait (Huntley et al. 1983). The presence of CI-CIII *C. glacialis* during the productive season, with notable maximum abundances from mid-June to mid-August, is a consistent feature in the Arctic (Grainger 1961; MacLellan 1967; Diel 1989; Eilertsen et al. 1989; Hansen et al. 1990). A flexible spawning behaviour pattern for *C. glacialis* is attained by long-term preservation of its reproductive potential, rapid mobilisation of ovaries during periods of favorable food conditions, and high rates of egg production (Hirche & Bohrer 1987; Hirche 1989). Although *C. glacialis* has been considered to spawn during the Arctic spring bloom, Smith (1990) showed that food was not required for spawning in the Fram

Strait in late March and early April. Cohorts produced during spawning in April would favour a generation time of one year, although spawning in May and June would be more suitable for a two-year life span (Slagstad & Tande 1990). Spawning, and the subsequent development of recruits in August and September, allows a fairly low chance of building up energy reserves for survival through the overwintering period; these recruits are likely to be considered as pseudocohorts (see Hirche 1989). Care should be taken when estimating the length of the life cycle based on embryonic development and the postulated rule of equiproportional development (see Corkett et al. 1986; Tande 1988a; Smith 1990; Pedersen & Tande 1991). However, the lack of frequent sampling on a seasonal basis of *C. glacialis* restricts our chances of tracing the periods of diapause, which should give two major overwintering stages (CIV and CV) in a two-year life cycle. Although the available data give no conclusive evidence for either an annual or a biennal life cycle, it could well be that the above reports mirror a flexible life cycle, where the circulation pattern, the extent of the productive period, and the timing of spawning determine the fraction of the population which enter a two-year life cycle.

A generally higher standing stock, without the extremely low winter biomass which is found for species with an annual life cycle, would be anticipated for a species with a two-year life cycle such as *C. glacialis*. This is clearly demonstrated in the data from the central Arctic Ocean where the total biomass of *C. glacialis* from three different depth strata showed very low seasonal variation during an investigation from January to December (Brodsky & Nitikin 1955; Grainger 1989). Slagstad & Tande (1990) presented model simulations of *C. glacialis* based on maximum population abundances in Arctic Water of the Barents Sea which yielded biomass estimates of approximately 5 g C m^{-2} for August (Fig. 6), as compared to a maximum of 4 g C m^{-2} for the total copepod community in Balsfjorden. The simulated values should be considered as maximum values since conservative estimates of 3.2 and 2.9 g C^{-2} are found for *C. glacialis* in Arctic Water east of Svalbard at the end of July 1984 (see Fig. 5C). Considerable regional variations in the population density of *C. glacialis* are found, where notably lower biomasses (2.15, 1.35 and 0.29 g C m^{-2} at Stations 1, 2, and 3, respectively) are recorded in the Polar Front in July 1987 (Fig. 5B). An even lower biomass (0.14 g C m^{-2}) was obtained in April 1986 in the same region (Fig. 5A). Compared to Atlantic Water in the Barents Sea, there is a tendency in the Arctic domain for a reduction in the quantitative importance of smaller copepods such as *Pseudocalanus* sp. and *Oithona similis* (Hassel 1986), which normally reach maximum biomass during late summer and autumn in Atlantic Water. These species appear to have been replaced in trophodynamic terms by the youngest year-group (CI-CIII) of *C. glacialis* which prevails during the oligotrophic Arctic summer and autumn.

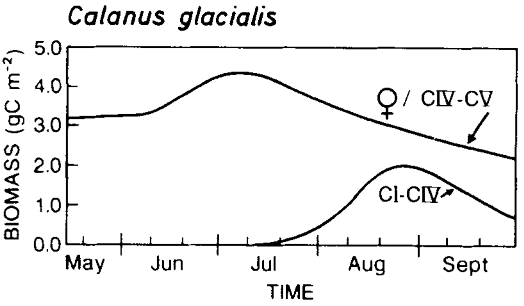

Fig. 6. Simulated standing stock of two year groups of *Calanus glacialis* (adult females/CIV/CV and CI-CIV, respectively) from May to September in the Barents Sea. The population dynamics in the model are based on a two year life cycle. See Slagstad & Tande (1990) for further details.

Potential production

Estimates of *Calanus glacialis* production have been conducted in a dynamic model by combining data from population and bioenergetic studies during the productive period in the Arctic (Slagstad & Tande 1990). Based on an estimate in primary production of 65 g C m^{-2}, the model indicates a *Calanus* production of 8.5 g C m^{-2} during a simulation period of 150 days at 78°N east of Svalbard. The physical-environmental data from the region of 78°N in 1984, where the ice started to disappear in May that year, was used in the standard run. Due to a two-year generation cycle, there is a bimodal seasonal production with a maximum during August when the cohort produced during the spring has developed to CI-CIV (Fig. 7). A tendency for a high degree of mismatch between the spring bloom and the subsequent buildup of copepod biomass in

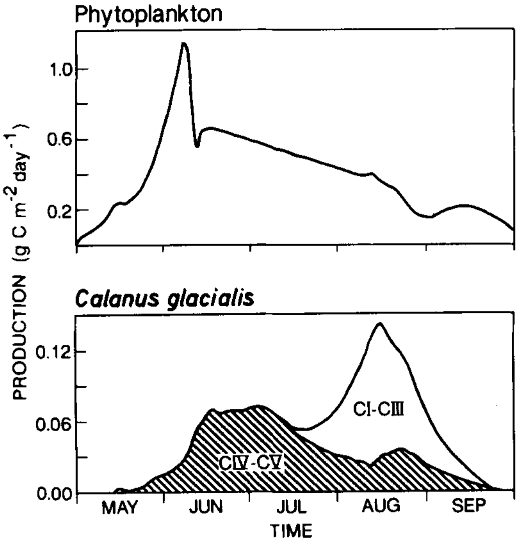

Fig. 7. Timing between copepod production in *Calanus glacialis* CIV-CV and CI-CIII during the productive period in the Arctic.

Balsfjorden is inherent in the data presented above. In the Arctic environment a two-year life cycle of *C. glacialis* should enhance an improved ability to exploit the spring bloom and reduce the general tendency for mismatch and the interspecific competition during the short productive season.

If the rate of energy accumulation of *Calanus glacialis* in the Arctic food web is considered in terms of lipid classes, well-defined patterns emerge. The proportion of wax esters increases from CI to CV of *C. glacialis*, and the highest proportions are apparent in CIV and CV (Henderson & Tande 1988). When this is considered in relation to the primary production in the Arctic, a substantial part of the wax ester deposition at the second trophic level tends to co-occur during the spring bloom (Fig. 7). In the Atlantic part of the Barents Sea and coastal waters of northern Norway *C. finmarchicus* (the spring and early summer form) and *Pseudocalanus* sp. (the late summer form) are the two quantitatively important copepods which rely on wax esters as their depot lipid. (Hopkins et al. 1984; Henderson & Tande unpubl. data; Norrbin et al. 1990). A two-year life cycle of *C. glacialis* gives rise to an analogous seasonal bimodal pattern of wax ester deposition in the Arctic as found in the boreal copepod community.

For herbivorous copepods, the extreme conditions in the Arctic should be viewed in relation to the large variability in the timing and duration of the periods in which food is available. This could be related directly to the interannual variation in the extension and retreat of ice during the productive season. Climatic changes with possible consequence for the production of *C. glacialis* can therefore be demonstrated by simulating different durations of the primary production period (Fig. 8). Based on the standard model simulation, five different situations were defined by changing the ice conditions. This was done by letting the ice cover disappear during one weak starting in the middle of each month from April to August, and simulate to the end of September. The potential production decreased from a maximum of 12.5 to 3 g C m^{-2} when the onset of primary production changed from the middle of April to the middle of August. The ice conditions which could change the productive period from 5.5 to 1.5 months thus have the potential to reduce the production of *C. glacialis* by a factor of 4. Although estimated production is higher than given in the standard

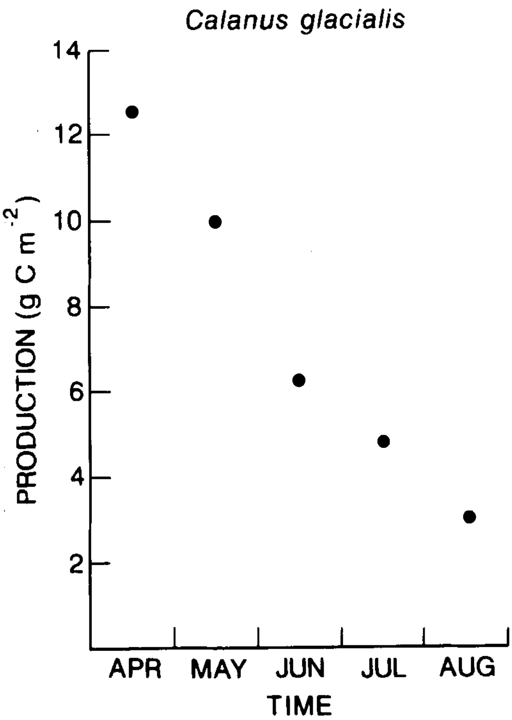

Fig. 8. Effect of timing of ice melt, controlling onset of algal bloom in water column on production of *Calanus glacialis*.

run for the model simulation in Slagstad & Tande (1990), the proportionate reduction in production should be considered relevant for this region. This means that during cold years, the climate would reduce the energy input to the lower trophic levels in the Arctic. This is not a consequence of low temperature by itself, but rather a result of the extent of the southern distribution of the ice during the productive season in the Barents Sea.

Calanus finmarchicus

In neritic waters from the North Sea, and in coastal waters of Norway to the Lofoten area, *Calanus finmarchicus* is considered to produce two generations per year (Sømme 1934; Østvedt 1955; Wiborg 1955; Marshall & Orr 1972; Matthews et al. 1978). An annual life cycle is found in oceanic waters in the North Atlantic Current from OWSI (59°N; 19°W), northwards to the coastal waters of northern Norway and to the Polar Front in the Barents Sea (Parsons & Lalli 1988; Tande 1982; Tande et al. 1985). The spawning behaviour of *C. finmarchicus* has recently been described in detail in fjord areas of northern Norway by Diel & Tande (1991). They have suggested that the onset of the phytoplankton spring bloom in the first days of April enhances the final maturation of ovaries and triggers the onset of the main spawning period. The overlap of the estimated minimum 4-week spawning period of the individuals leads to a main reproductive phase of the population of approximately 3 weeks duration. During this period mean clutch size and spawning frequency are maximal.

Conclusive patterns of regional and seasonal variations in abundance and biomass are hampered because of the relatively restricted numbers of appropriate time series of field data from the Barents Sea. Maximum abundances of *C. finmarchicus* are found during the annual recruitment period from mid-May to the end of June (Tande & Slagstad 1991). The peak in the biomass shifts slightly, occurring two or three weeks later in the Barents Sea compared to Balsfjorden, when the population has moulted to CIV and CV (Tande 1982; Tande & Slagstad 1991). An abundance of CIII and CIV, when they appeared as the highest proportions of the population, varied from 2–130 × 10^3 individuals m^{-2} along a transect from 73 to 76°N in central parts of the Barents Sea at the end of June 1981 (Hassel 1986). The abundance of CI to CIV *C. finmarchicus* monitored from the end of May to mid-June 1987 from 73 to 75°N to the east of Bjørnøya, at an earlier stage in the annual recruitment period than above, varied by a factor of 10 (from 3–30 × 10^3) within the various developmental stages (Unstad & Tande 1991 this volume).

Population studies of *Calanus finmarchicus* in March, April, and May 1989 from the Atlantic Current in the western part of the Barents Sea (Fig. 9) show that males outnumbered females in March, i.e. the period of insemination occurs later than in Balsfjorden (Tande & Hopkins 1981; Tande 1982). The temperature was increased from 4 to 6°C at Station 6, and from 3.5 to 5.5°C at Station 12 from March to May. Regional variations in the sex ratio at the different stations within the study region appear to be consistent, and there is a less skewed sex ratio in favour of males at Stations 6, 7, 11, and 13 in March and April. On 10 May the recruitment generation of *C. finmarchicus* was found as CI and CII at three of these four stations. This indicates that the onset of spawning and the subsequent build-up of the

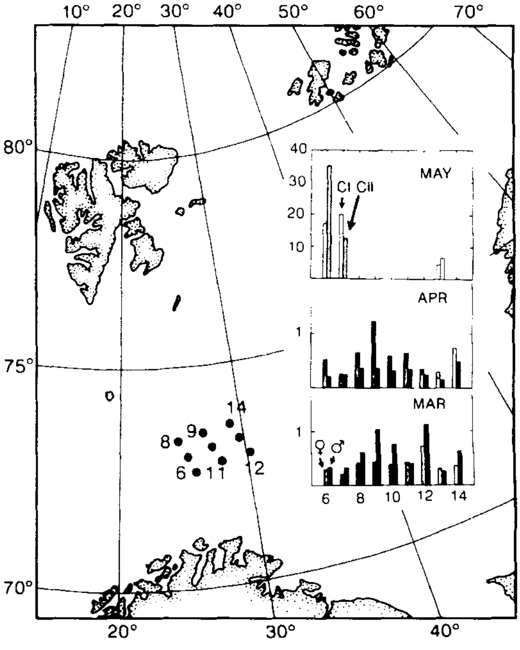

Fig. 9. Regional variation in the abundance (m^{-2}) of *Calanus finmarchicus* males and females during March and April, and the subsequent build-up of CI and CII in May 1989 in oceanic waters of the Barents Sea.

recruitment generation could differ by two weeks in open oceanic waters in the Barents Sea. This emphasises the importance of monitoring the biological system in relation to the hydrographic conditions in order to obtain a more precise differentiation of the productive regime in the Atlantic part of the Barents Sea.

A method of estimating the production of *Calanus finmarchicus* in boreal waters has been described by Tande & Slagstad (1991). Model simulations estimate the annual primary production to 70 g C m^{-2} for open oceanic waters in the Atlantic region of the sea; this is in general agreement with figures provided by Rey et al. (1987). The estimation of *Calanus* production is based on physical data from 1983 (Fig. 10), starting with a spawning stock of 2000 adult females m^{-2}. Population parameters scale the abundance of CI-CV according to the maximum recorded in the Atlantic region of the sea in 1983 (Skjoldal et al. 1987) and give a potential production of 8.5 g C m^{-2} (Tande & Slagstad 1991). Copepodite Stages IV and V are responsible for the largest proportion of this production and occur during the culmination period from mid-June to mid-July in the standard run. In terms of lipid deposition in *C. finmarchicus*, wax esters are laid down in increasing proportions during the copepodite growth period (Henderson & Tande, unpubl. results). This is analogous to the situation described for the Arctic domain, in which the time period of wax ester accumulation takes place fairly early in the productive period and is coupled to the intensive growth and production period in *C. finmarchicus*.

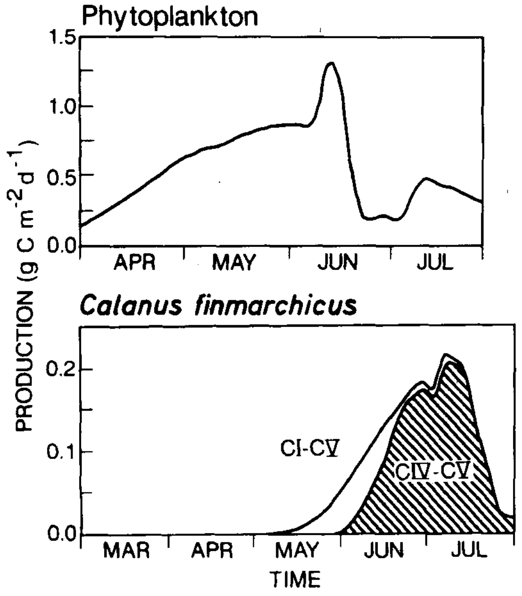

Fig. 10. Timing between the copepod production in *Calanus finmarchicus* (CI-CV and CIV-CV, respectively) and the culmination of the spring bloom in Atlantic waters.

Regional variations in estimates of *C. finmarchicus* production in temperate and boreal waters have been reviewed in Tande & Slagstad (1991). Recently, it has been suggested that climatic events play a major role in the interannual variability of copepod populations in the Bering Sea (Vidal & Smith 1986). A higher biomass of smaller copepod forms (*Pseudocalanus* spp. and *Oithona similis*) was observed in warm years than in cold years on the middle shelf in the southeastern Bering Sea (Vidal & Smith 1986). This variation is related to size-dependent differences in metabolic rates, and copepods with small body sizes are proportionally more affected by temperature than by food supply (Vidal 1980a, b). This is exemplified for *C. finmarchicus* in the Barents Sea, where the standard model predicts a production of 12, 8, and 4 g C m^{-2} at temperatures of 7, 5, and 3°C, respectively (Fig. 11). Mortality according to the model is 0.11% d^{-1} for the period from NI to CI. For CII-CIII, CIV, and CV, the mortality is set at 0.077, 0.055, and 0.004, respectively (Tande & Slagstad 1991). This means that lower temperature would increase the stage durations and thus the total mortality of the recruiting generation.

Support for the increase in production at high environmental temperatures is not found as an increase in biomass of *C. finmarchicus* during the summer in warm years in the Barents Sea.

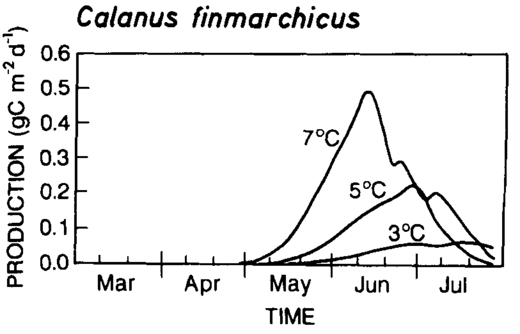

Fig. 11. Sensitivity analysis of the effect of temperature on the potential productivity in *Calanus finmarchicus*.

Abundances at 74, 75, and 76°N along a transect in the Polar Front region in the beginning of June 1982 and 1983 differed in favour of the former year by a factor of 100 (Skjoldal et al. 1987). Although 1983 was generally a warmer year than 1982, there were temperatures of about 3.5 and 2.5°C, respectively, in the beginning of June in the uppermost 100 m at 75°N. These interannual differences should be interpreted with caution since the area of sampling is located in the Polar Front region where the biomass consisted both of *C. glacialis* and *C. finmarchicus* (Skjoldal et al. 1987). For copepods with one generation per year, the overwintering stock of mature females is considered important for the subsequent production period (Tande & Slagstad 1991), which also links predation to the copepod production the following year. Although the differences in biomass found in the summer period from 1979 to 1984 could be explained by various factors, large interannual variations in copepod production are highly probably in the Barents Sea.

Recently, the mortality and developmental rates of nauplii and copepodite stages of *C. finmarchicus* from neritic waters in northern Norway have been obtained both at constant and continuously changing temperatures (Pedersen & Tande 1991). The temperature regimes in the experiments simulated three different rates of increase from 2°C: 0.2, 0.1, and 0°C d^{-1}, which are within the range of variations in high latitude environments. The resulting mortality rates showed that increases in temperature yielded low mortalities for transition from nauplii and to copepodite Stage I. Thus an increase in temperature would reduce natural mortality in *C. finmarchicus* during the recruitment period. Populations which experienced 2°C continuously showed in general higher mortality rates in addition to arrested development and mass mortality after 20 days of incubation. The temperature-dependent mortality rate is, at the moment, difficult to quantify in ecological terms. The situation is complicated by a possible acclimation effect of the overwintering temperature experienced by the adult females (Pedersen & Tande 1991). The temperatures experienced by overwintering females appear to modify the relationship between temperature and developmental rates of the offspring. This means that there is a certain degree of physiological plasticity to temperature in *C. finmarchicus* which could be of ecological relevance to the species in the Barents Sea.

Vertical organisation and temporal shifts in the lower food chain.

The temporal succession and match-mismatch between primary production and the growth cycles of *Calanus glacialis* and *C. finmarchicus*, described above reinforce the question of food limitation of these copepods during the productive period in the Barents Sea.

The highly layered structure of the pelagic ecosystem has been suggested as the primary spatial variance in the ocean (Longhurst 1981). In coastal waters of northern Norway and in the Barents Sea the seasonal (ontogenetic) vertical migration patterns in *C. finmarchicus* tend to coincide with the annual generation cycle (Unstad & Tande 1991). In these areas CI-CIII tended to aggregate in the uppermost waters in May and June (Tande 1988b; Unstad & Tande 1991). Ontogenetic vertical migrations were apparent in almost all locations studied, and the maximum abundance was, to a variable degree, associated with the maximum of algal biomass. The magnitude of diurnal vertical migration varied, and considerable differences in vertical translocations in the abundance were found in Malangen as compared to Grøtsund and Balsfjorden (Tande 1988b). In the Barents Sea, the vertical separation of copepodite stages tended to increase at locations with the absence of a well-defined phytoplankton maximum, both at high and low phytoplankton standing crops. In waters where *C. finmarchicus* and *C. glacialis* coexisted at high population densities, a tendency toward a clear bimodal distribution pattern was found which could facilitate a decrease in competition for similar food resources.

The phytoplankton biomass is often both vertically and regionally dominated by the prymnesiophyte *Phaeocystis pouchetii* during the most intensive growth and production period of *C. finmarchicus*. Given a suitable prey size *C. finmarchicus* grazed on both diatoms and colonies of the gelatinous algae at equal rates in laboratory studies (Hansen et al. 1991). A linear relationship between gut content and food concentrations below 10 μg plant pigment l^{-1} was found. These data emphasise that ingestion in *C. finmarchicus* might be linearly proportional to ambient food concentration in May and June (cf. Fig. 10). Although *P. pouchetii* is likely to sustain growth in all life stages of *C. finmarchicus* during the culmination period and the early part of the oligotrophic summer period, substantial regional variations in algal biomass and *C. finmarchicus* abundance was found both in the fjords in northern Norway during 1986 (Tande 1988b) and in the Barents Sea in 1987 (Unstad & Tande 1991). Longterm interannual variations in abundance and biomass of *Calanus* spp. are found during the summer periods from 1959 to 1977 (Degtereva 1979) and from 1979 to 1984 (Skjoldal & Rey 1989) in the southwestern and central parts of the Barents Sea, respectively. The annual production of *Calanus* has been found to be positively correlated to the size of the overwintering stock of adult females both in model analysis (Tande & Slagstad 1991) and also in field studies from the North Sea (Colebrook 1979). Thus food-limited growth and production by *C. finmarchicus* in Atlantic Water of the Barents Sea is more likely to take place in regions with high copepod abundances than through mismatch in the cycles between the diatoms, *P. pouchetii*, and the copepod.

The feeding conditions of the different life stages of *C. glacialis* during the oligotrophic period in the Arctic are defined to a large extent by the algal species sedimenting from the euphotic layer (c.f. Eilertsen et al. 1989). Colonial forms such as *P. pouchetii* and the mixotroph *Dinobryon* sp. are common in the layer, although low numbers of diatoms could generally be indicative of selective grazing. In situ feeding rates above those expected from ambient diatom concentrations are found at locations where colonial forms prevail, increasing the trophodynamic importance of the colonial forms (Hansen et al. 1990). Alternative food organisms have not been considered in these studies, but diatoms, flagellates, and ciliates were found in the diets of *Calanus* spp. in polynyas, at the ice edge and in open waters in June and July in the Fram Strait (Barthel 1988). Recent data show that Protistan plankton consume a greater fraction of plant production than Metazoa, and Protista would alter the overall quantity and vertical pattern of carbon flow between plant producers and *Calanus* spp. in the Arctic.

A deep-water chlorophyll maximum layer (SCM) is usually formed around the nutricline during the Arctic summer period by a gradual descent of the spring surface blooms (Tande & Båmstedt 1985; Eilertsen et al. 1989; Longhurst & Harrison 1989). The SCM is a temporal phenomenon which tracks the deepening mixed layer, lasts during the oligotrophic period, and is eroded at the end of the productive period in autumn. The situation has been clearly demonstrated in Arctic waters east of Svalbard at the end of July (Eilertsen et al. 1989). Here the vertical profiles in algal biomass (in terms of carbon) tracks the phytoplankton carbon assimilation, although the data do not facilitate a separation of the production maximum from the algal biomass maximum. However, the biomass of the principal herbivores (i.e. *Calanus* spp.) are found within the algal production layer, although they are shifted slightly towards deeper waters. Ontogenetic differences in vertical distributions within both *C. glacialis* and *C. hyperboreus* offset the vertical profiles of grazing and algal production to an even larger extent. Vertical profiles of algal production and grazing vary extensively in the region of the Polar Front during the *post-bloom* period (Hansen et al. 1990). This emphasises the anticipated spatial heterogeneity which is often found in the vertical coupling of algal production and zooplankton grazing in frontal systems due to variability in the physical environment. On the other hand, the striking offset of the vertical distribution of the primary producers relative to macrozooplankton during the oligotrophic Arctic summer period favours the existence of the SCM. Therefore, the question of food limitation in *C. glacialis* in the Arctic environment should be viewed in an evolutionary context where the feeding behaviour, vertical behavior and life cycle strategy are adjusted to facilitate an optimal harvesting strategy of the Arctic phytoplankton community both on a temporal and a regional scale.

Calanus productivity: an interplay between endemic and advective processes

The large-scale periodic changes in temperature are shown by temperature anomalies (Fig. 12) during a 25 years period in the Kola section 33°30'E) in the Barents Sea (Midttun & Loeng 1987). Warm and cold periods alternate in periods of 3–5 years and are closely related to the ice conditions (Blindheim & Loeng 1981). Midttun & Loeng (1987) have suggested that these variations are related to variations in the inflowing Atlantic Water. Thus, temperature changes in the eastern part of the Barents Sea usually occur one year later than in the western part (Loeng et al. 1983).

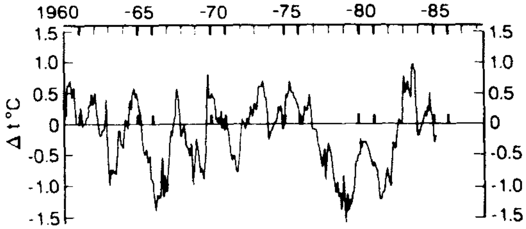

Fig. 12. Sea temperature anomalies during the period from 1960 to 1985 along the Kola section in the Barents Sea. Redrawn from Midttun & Loeng (1987).

To what extent the temperature changes shown in Fig. 12 reflect variations in inflowing activity or properties of the Atlantic Water is debatable. However, it is obvious that the Atlantic Water is modified by local processes in the Barents Sea, where cooling and ice formation result in water of higher density. Cooling and ice formation change inflowing Atlantic Water into dense bottom water, which promotes outflow through the channels (particularly through Bjørnøyrenna) leading out from the Barents Sea. A large inflow would then be followed by a period of cooling and modification of the Atlantic Water. This could be one reason for the apparently cyclic variation in the ocean climate particularly in the Atlantic region of the Barents Sea.

The functioning of *Calanus glacialis* and *C. finmarchicus* within these physical conditions could be described in different scenarios. Extremely cold years are associated with a southern distribution of the ice during the spring. This situation would tend to decrease the potential secondary production in Arctic and Atlantic waters, but through different mechanisms. The Arctic domain should be considered as an unpredictive environment for *C. glacialis* since the northward-flowing water currents in the eastern area would counteract the anticipated increase in production following the ice withdrawal. This would tend to delay the onset of the spring bloom with a consequently negative effect on the potential production of the proportion of the population present in these regions. The opposite situation could be found for *C. glacialis* in the western region where the Arctic Water flows in the opposite direction. Cold periods would not tend to alter the overall pattern of primary production in the Atlantic Water, but would tend to lower the potential productivity in "*finmarchicus*" water more directly through temperature. The cooling would enhance the negative effect on development and mortality rates because the anticipated temperature increase during the spring and early summer would be low or absent in certain regions. Advection would increase the transport of biomass to the Barents Sea, increase the extent of the productive "*finmarchicus*" area, and promote the endemic productivity in both the Atlantic and the Arctic region of the Barents Sea.

The food chain from *Calanus* to planktivorous fish and gelatinous zooplankters is therefore dependent upon productivity changes endemic to the sea and upon advection of biomass from Polar Water, the Norwegian Sea, and the Norwegian Coastal Current. The Barents Sea is considered as a nursery area for the young year classes of Atlanto-Scandian herring (Dragesund et al. 1980). Capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*) are endemic planktivorous fishes inhabiting both Atlantic and Arctic waters (Hamre 1985; Monstad & Gjøsæther 1987). Although large fluctuations in the stocks have been detected during the 1970 and 1980s, Skjoldal & Rey (1989) believe that these two species act as competitors on the zooplankton biomass and production. The interannual variability in plankton biomass found in the different regions of the sea (i.e. Degtereva 1979; Skjoldal & Rey 1989) is probably related to large scale processes. The way in which these trophodynamic couplings are expressed in quantitative dynamic terms is at present largely unknown. In order to substantiate these important links, future research in the Barents Sea should be designed to cover three topics: firstly, a description of the dynamics in the large-scale advective processes, especially from the North Atlantic and the Norwegian Coastal currents with monitoring of the biomass involved and the biological consequences for the different regions in the Barents Sea; secondly, a more elaborate understanding of the harvesting strategy of fish on the principal planktivores on copepods and krill in the different regions of the Barents Sea proper; and thirdly, experimental studies in conjunction with field investigations in order to further substantiate the effect of climate on the biological rate processes among key species in the Atlantic region of the Barents Sea.

Acknowledgements. – This work is part of the Pro Mare programme and was financially supported in part by the Norwegian Fisheries Research Council (NFFR). The author wishes to thank two anonymous reviewers for valuable comments on the manuscript and D. Slagstad for performing the simulation test and for the stimulating discussions.

References

Ådlandsvik, V. 1989: Wind-driven variations in the Atlantic inflow to the Barents Sea. *Coun. Meet. Int. Coun. Expor. Sea (C:18)*, 1–12.

Barthel, K.-G. 1988: Feeding of three *Calanus* species on different phytoplankton assemblages in the Greenland Sea. *Meeresforsch. 32*, 92–106.

Berggreen, U., Hansen, B. & Kiørboe, T. 1988: Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. *Mar. Biol. 99*, 341–352.

Blindheim, J. & Loeng, H. 1981: On the variability of Atlantic influence in the Norwegian and Barents Sea. *Fisk.dir. Skr. Ser. Havunders. 17*, 161–189.

Brodsky, K. A. & Nitikin, M. M. 1955: Hydrobiological work. Pp. 401–465 in Somov, M. M. (ed.): *Materialy Nabliudenii Nauchno-issledovatel Skoi Dreifuiushchel Stantsii 1950/51 Goda.* Izd. "Morskoi Transport" 1954–1955, 1 (Transl. Am. Meteorol. Soc.).

Colebrook, J. M. 1979: Continuous plankton records: seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea. *Mar. Biol. 51*, 23–32.

Conover, R. J. 1988: Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the Northern Hemisphere. *Hydrobiologia 167/168*, 127–142.

Corkett, C. J., McLaren, I. A. & Sevigny, J.-M. 1986: The rearing of the marine calanoid copepods *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov and *C. hyperboreus* Krøyer with comment on the equiproportional rule. Pp. 539–546 in Schriver, G., Schminke & Shih, H. K. (eds.): *Proceedings of the Second International Conference on Copepoda, Ottawa.*

Cushing, D. H. & Dixon, R. R. 1976: The biological response in the sea to climatic changes. *Adv. Mar. Biol. 14*, 1–122.

Davis, C. S. 1984: Predatory control of copepod seasonal cycles on Georges Bank. *Mar. Biol. 82*, 31–40.

Degtereva, A. A. 1979: Regularities of quantitative development of zooplankton in the Barents Sea. Trudy PINRO, Murmansk *43*, 22–53 (in Russian).

Dickson, R. R., Midttun, L. & Mukhin, A. I. 1970: The hydrographic conditions in the Barents Sea in August-September 1965–1968. Pp. 3–24 in Dragesund, O. (ed.): *International 0-group fish surveys in the Barents Sea 1965–1968.* Int. Coun. Explor. Sea. Cooperative Res. Rep. Ser A, No. 18.

Diel, S. 1989: Zur Lebensgeschichte dominanter Copepodearten (*Calanus finmarchicus, C. glacialis, C. hyperboreus, Metridia longa*) in Framstrasse. Ph.D. thesis, Christian Albrechts University, Kiel. 140 pp.

Diel, S. & Tande, K. S. 1991: Does the spawning of *Calanus finmarchicus* in high latitude follow a predictable pattern? A case study. *Mar. Biol.* In press.

Dragesund, O., Hamre, J., & Ultang, Ø. 1980: Biology and population dynamics of the Norwegian spring spawning herring. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer 177*, 43–71.

Eilertsen, H. S. 1983: *Planteplankton før og etter vassdragsreguleringen i Skjomen 1970–1972.* Rådgivende utvalg for fjordundersøkelser, Skjomenprosjektet, Oslo. 60 pp. (in Norwegian)

Eilertsen, H. C. & Tassen, J. P. 1984: Investigations on the plankton community of Balsfjorden, northern Norway. The phytoplankton 1976–1978. Environmental factors, dynamics of growth, and primary production. *Sarsia 69*, 1–15.

Eilertsen, H. C., Tande, K. S. & Hegseth, E. N. 1989: Potential of herbivorous copepods for regulating the spring phytoplankton bloom in the Barents Sea. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer 188*, 154–163.

Eilertsen, H. C., Schei, B. & Taasen, J. P. 1981: Investigations on the plankton community of Balsfjorden, northern Norway. The phytoplankton 1976–1978. Abundance, species composition, and succession. *Sarsia 66*, 129–141.

Eilertsen, H. C., Tande, K. S. & Taasen, J. P. 1989: Vertical distribution of primary production and grazing by *Calanus glacialis* Jaschnov and *C. hyperboreus* Krøyer in Arctic waters (Barents Sea). *Polar Biol. 9*, 253–260.

Eilertsen, H. C., Taasen, J. P. & Weslawski, J. M. 1989: Phytoplankton studies in the fjords of West Spitsbergen: physical environment and production in spring and summer. *J. Plank. Res. 11*, 1245–1260.

Eilertsen, H. C., Hopkins, C. C. E., Falk-Petersen, S. & Tande, K. S. 1981: Ecological investigations on the plankton community of Balsfjorden, northern Norway. Program for the project, study area, topography, and physical environment. *Sarsia 66*, 25–34.

Evans, F. 1977: Seasonal density and production estimates of the commoner planktonic copepods of Northumberland coastal waters. *Estuar. Coastal Mar. Sci. 5*, 223–241.

Gaarder, K. R. 1938: Phytoplankton studies from the Tromsø district 1930–31. *Tromsø Mus. Årsh. 55(1)*, 1–159.

Grainger, E. H. 1961: The copepods *Calanus glacialis* (Jaschnov) and *Calanus finmarchicus* (Gunnerus) in Canadian Subarctic waters. *J. Fish. Res. Bd. Can. 18*, 663–678.

Grainger, E. H. 1989: Vertical distribution of zooplankton in the central Arctic Ocean. Pp. 48–60 in Rey, L., Alexander, V. (eds.): *Proc. 6th Conf. Com. Arctique Internat.*, 13–15 May 1985. E. J. Bill, Leiden.

Grønvik, S. & Hopkins, C. C. E. 1984: Ecological investigations of the zooplankton community of Balsfjorden, northern Norway: generation cycle, seasonal vertical distribution, and seasonal variations in body weight and carbon and nitrogen content of the copepod *Metridia longa* (Lubbock). *J. Exp. Mar. Biol. Ecol. 80*, 93–107.

Hamre, J. 1985: Assessment and management of Barents Sea capelin. Pp. 5–24 in H. Gjøsæter (ed.): *Proc. Soviet-Norwegian Symp. Barents Sea Capelin.* Institute of Marine Research, Bergen, Norway 1989.

Hansen, B., Tande, K. S. & Berggreen, U. C. 1991: On the trophic fate of *Phaeocystis pouchetii* (Hariot) III. Functional responses in grazing demonstrated on juvenile stages of *Calanus finmarchicus* (Copepoda) fed diatoms and *Phaeocystis. J. Plankton Res. 12*, 1177–1187.

Hansen, B., Berggreen, U., Tande, K. S. & Eilertsen, H. C. 1990: Post-bloom grazing by *Calanus glacialis, C. finmarchichus* and *C. hyperboreus* in the region of the Polar Front, Barents Sea. *Mar. Biol. 104*, 5–14.

Hassel, A. 1986: Seasonal changes in zooplankton composition in the Barents Sea, with special attention to *Calanus* spp. (Copepoda). *J. Plankton Res. 8*, 329–339.

Henderson, R. J. & Tande, K. S. 1988: Lipid composition of copepodite stages and adult females of *Calanus glacialis* in Arctic waters of the Barents Sea. *Polar Biol. 8*, 333–339.

Heimdal, B. R. 1974: Composition and abundance of phytoplankton in the Ullsfjord area, North Norway. *Astarte 7*, 17–42.

Helland-Hansen, B. & Nansen, F. 1909: The Norwegian Sea. *Fisk.dir. Skr. Ser. Havunders. 2(2)*, 1–360.

Hirche, H.-J. 1989: Egg production of the Arctic copepod *Calanus glacialis*: laboratory experiments. *Mar. Biol. 103*, 311–318.

Hirche, H.-J. & Bohrer, R. N. 1987: Reproduction of the Arctic copepod *Calanus glacialis* in Fram Strait. *Mar. Biol. 94*, 11–17.

Hopkins, C. C. E., Tande, K. S., Grønvik, S. & Sargent, J. R. 1984: Ecological investigations of the zooplankton community of Balsfjorden, northern Norway: an analysis of growth and overwintering tactics in relation to niche and environment in *Metridia longa* (Lubbock), *Calanus finmarchicus* (Gunnerus) *Thysanoessa inermis* (Krøyer) and *T. raschii* (M. Sars). *J. Exp. Mar. Biol. Ecol. 82*, 77–99.

Hopkins, C. C. E., Tande, K. S., Sargent, J. R. & Schweder, T. 1985: Ecological investigations of the zooplankton community of Balsfjorden, northern Norway: growth, and quantification of condition, in relation to overwintering and food supply in *Metridia longa, Calanus finmarchicus, Thysanoessa inermis* and *T. raschii*. Pp. 83–101 in Gray, J. S. and Christiansen, M. (eds.): *Marine Biology of polar regions and effects of stress on marine organisms*. J. Wiley and Sons.

Huntley, M., Strong, K. W. & Dengler, A. T. 1983: Dynamic and community structure of zooplankton in the Davis Strait and northern Laborador Sea. *Arctic 36*, 143–161.

Jaschnov, W. A. 1967: Water masses and plankton. I. Species of *Calanus finmarchicus* s.l. as indicators of definite water masses. *Zool. Zh. 40*, 1314–1334 (in Russian).

Jaschnov, W. A. 1970: Distribution of *Calanus* species in the seas of the Northern Hemisphere. *Int. Rev. Ges. Hydrobiol. Hydrogr. 55*, 197–212.

Jaschnov, W. A. 1972: On the systematic status of *Calanus glacialis, Calanus finmarchicus*, and *Calanus helgolandicus*. *Crustaceana 22*, 279–284.

Klein Breteler, W. C. M., Franz, H. G., & Gonzalez, S. R. 1982: Growth and development of four calanoid species under experimental and natural conditions. *Neth. J. Sea Res. 16*, 195–207.

Lindley, J. A. 1990. Distribution of overwintering calanoid copepod eggs in sea-bed sediments around southern Britain. *Mar. Biol. 104*, 209–217.

Loeng, H. 1991. Features of the physical oceanographic conditions of the Barents Sea. *Polar Res.* Pp. 5–18 in Sakshaug, E., Hopkins, C. C. E. & Øritsland, N. A. (eds.): Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990. *Polar Research 10(1)*.

Loeng, H. & Midttun, L. 1984: Climatic variations in the Barents Sea during the 1970's. *Coun. Meet. Int. Coun. Explor Mer* (G:15). 1–10 (mimeographed).

Loeng, H. & Vinje, T. E. 1979: On the sea ice conditions in the Greenland and the Barents seas. Pp. 163–176 in *Proc. 5th Internat. Conf. Port Ocean Engineering and Arctic Conditions*. The Norwegian Institute of Technology, University of Trondheim.

Loeng, H., Nakken, O. & Raknes, A. 1983: Variations in the geographical distribution of cod in the Barents Sea in the period 1977-1981. *Fisken og Havet.* 1981 (4). 1–16 (in Norwegian, English abstract).

Longhurst, A. R. 1981: BIOSTAT, an experiment in Ocean Plankton Ecology. *Bedford Institute of Oceanography, Report Series BI-R-81-13*, 1–105.

Longhurst, A. R. & Harrison, W. G. 1989: The biological pump: Profiles of plankton production and consumption in the upper ocean. *Progr. Oceanog. 22*, 47–123.

McLaren, I. A., Tremblay, M. J., Corkett, C. J. & Roff, J. C. 1989: Copepod production on the Scotian Shelf based on life-history analysis and laboratory rearings. *Can. J. Fish. Aquat. Sci. 46*, 560–582.

MacLellan, D. C. 1967: The annual cycle of certain calanoid species in West Greenland. *Can. J. Zool. 45*, 101–115.

Marshall, S. M. & Orr, A. P. 1972: *The biology of a marine copepod Calanus finmarchicus* (Gunnerus). Oliver & Boyd, Edinburgh. 195 pp.

Matthews, J. B. L. 1967: Continuous plankton records: the geographical and seasonal distribution of *Calanus finmarchicus* s.l. in the North Atlantic. *Bull. Mar. Ecol. 6*, 252–273.

Matthews, J. B. L., Hestad, L. & Bakke, J. L. W. 1978: Ecological studies in Korsfjorden, western Norway. The generations and stocks of *Calanus hyperboreus* and *C. finmarchicus* in 1971–1974. *Oceanologica Acta 1*, 277–284.

Midttun, L. & Loeng, H. 1987: Climatic variations in the Barents Sea. Pp. 113–27 in Loeng, H. (ed.): *The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea.* Proc. 3rd Soviet-Norwegian Symp., Murmansk 26–28 May 1986. Inst. Mar. Res., Bergen.

Monstad, T. & Gjøsæter, H. 1987. Observations on polar cod (*Boreogadus saida*) in the Barents Sea 1973 to 1986. *ICES C. M. 1987/G:13.*

Neumenko, E. A. 1979: Life cycles of some copepods from the southeastern Bering Sea. *Hydrobiol. J. 15*, 25–27.

Norrbin, M. F. 1987: Overwintering strategies of *Pseudocalanus elongatus* Boeck and *Acartia longiremis* Lilljeb. in Balsfjorden, northern Norway. Seasonal abundance, size variation, sex ratios, and gonad maturation. Fil. lic. thesis, University of Gothenburg.

Norrbin, M. F., Olsen, R.-E. & Tande, K. S. 1990: Seasonal variation in lipid class and fatty acid compositions of two small copepods in Balsfjorden, northern Norway. *Mar. Biol. 105*, 205–211.

Østvedt, O. J. 1955: Zooplankton investigations from weather ship M in the Norwegian Sea, 1948–49. *Hvalr. Skrifter 40*, 1–93.

Parsons, T. R. & Lalli, C. M. 1988: Comparative oceanic ecology of the plankton communities of the subarctic Atlantic and Pacific Oceans. *Oceanogr. Mar. Biol. Ann. Rev. 26*, 317–359.

Pedersen, G. & Tande, K. S. 1991: Physiological plasticity to temperature in *Calanus finmarchicus*. Reality or artefact? *J. Exp. Mar. Biol. Ecol.* In press.

Pertzova, N. M. 1974: Life cycle and ecology of a thermophilous copepod *Centrophages hamatus* in the White Sea. *Zool. Zh. 53*, 1013–1022.

Prygunkova, R. V. 1969: The development cycle of *Calanus glacialis* in the White Sea. *Dokl. Akad. Nauk SSSR 182*, 1447–1450.

Rey, F., Skjoldal, H. R. & Slagstad, D. 1987: Primary production in relation to climatic changes in the Barents Sea. Pp. 29–46 in Loeng, H. (ed.): *The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea.* Proc. 3rd Soviet-Norwegian Symp., Murmansk 26–28 May 1986. Inst. Mar. Res., Bergen.

Runge, J. A., McLaren, I. A., Corkett, C. J., Bohrer, R. N.

& Kislow, J. A. 1986: Moulting rates and cohort development of *Calanus finmarchicus* and *C. glacialis* in the sea off southwest Nova Scotia. *Mar. Biol. 86*, 241–246.

Sakshaug, E. 1972: Phytoplankton investigations in Trondheimsfjord, 1963–1966. *K. Norske Videns. Selsk. Skr. 1972(1)*, 1–56.

Sambrotto, R. N., Niebauer, H. J., Goering, J. J. & Iverson, R. L. 1986: Relationships among vertical mixing, nitrate uptake, and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. *Cont. Shelf Res. 5*, 161–198.

Schei, B. 1974: Phytoplankton investigations in Skjomen, a fjord in North Norway, 1970–1971. *Astarte 7*, 43–59.

Skjoldal, H. R. & Rey, F. 1989: Pelagic production and variability of the Barents Sea ecosystem. Pp. 241–286 in Sherman, K. & Alexander, L. A. (eds.): *Biomass yields and geography of large marine ecosystems.* AAAS Selected Symposium 111. Westview Press.

Skjoldal, H. R., Hassel, A., Rey, F. & Loeng, H. 1987: Spring phytoplankton and zooplankton reproduction in the central Barents Sea in the period 1979–1984. Pp. 59–89 in Loeng, H. (ed.). *The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea.* Proc. 3rd Soviet-Norwegian Symp., Murmansk 26–28 May 1986. Inst. Mar. Res., Bergen.

Slagstad, D., & Tande, K. S. 1990: Growth and production dynamics of *Calanus glacialis* in an Arctic food web. *Mar. Ecol. Prog. Ser. 63*, 189–199.

Smith, S. L. 1990: Egg production and feeding by copepods prior to the spring bloom of phytoplankton in Fram Strait, Greenland Sea. *Mar. Biol. 106*, 59–69.

Sømme, J. D. 1934: Animal plankton of the Norwegian coast waters and the open sea: I. Production of *Calanus finmarchicus* (Gunnerus) and *Calanus hyperboreus* (Krøyer) in the Lofoten area. *Rep. Norw. Fish. Invest. 4(9)*, 1–163.

Sverdrup, H. U. 1953: On conditions for the vernal blooming of phytoplankton. *J. Cons. Perm. Int. Explor. Mer 18*, 287–295.

Tande, K. S. 1982. Ecological investigations on the zooplankton community in Balsfjorden, northern Norway: generation cycles, and variations in body weight and body content of carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus finmarchicus* (Gunnerus). *J. Exp. Mar. Biol. Ecol. 62*, 129–142.

Tande, K. S. 1988a: Aspects of developmental and mortality rates in *Calanus finmarchicus* related to equiproportional development. *Mar. Ecol. Prog. Ser. 44*, 51–58.

Tande, K. S. 1988b: An evaluation of factors affecting vertical distribution among recruits of *Calanus finmarchicus* in three adjacent high-latitude localities. *Hydrobiologia 167/168*, 115–126.

Tande, K. S. & Båmstedt, U. 1985: Grazing rates of the copepods *Calanus glacialis* and *C. finmarchicus* in Arctic waters of the Barents Sea. *Mar. Biol. 87*, 251–258.

Tande, K. S. & Grønvik, S. 1983: Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: sex ratio and gonad maturation cycle in the copepod *Metridia longa* (Lubbock). *J. Exp. Mar. Biol. Ecol. 71*, 43–54.

Tande, K. S. & Hopkins, C. C. E. 1981: Ecological investigations on the zoo plankton community in Balsfjorden, northern Norway: the genital system in *Calanus finmarchicus* and the role of gonad development in overwintering strategy. *Mar. Biol. 63*, 159–164.

Tande, K. S. & Slagstad, D. 1991: Regional and interannual variations in biomass and productivity of *Calanus finmarchicus* in subarctic environments. *Oceanologica Acta.* In press.

Tande, K. S., Hassel, A. & Slagstad, D. 1985: Gonad maturation and possible life cycle strategies in *Calanus finmarchicus* and *C. glacialis* in the northwestern part of the Barents Sea. Pp. 141–157 in Gray, J. S. and Christiansen, M. (eds.): *Marine Biology of polar regions and effects of stress on marine organisms.* J. Wiley and Sons.

Unstad, K. & Tande, K. S. 1991: Depth distribution of *Calanus finmarchicus* and *C. glacialis* in relation to environmental conditions in the Barents Sea. Pp. 409–420 in Sakshaug, E., Hopkins, C. C. E. & Øritsland, N. A. (eds.): Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990. *Polar Research 10(2).*

Vidal, J. 1980a: Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. *Mar. Biol. 56*, 135–146.

Vidal, J. 1980b: Physioecology of zooplankton. II. Effects of phytoplankton concentration, temperature, and body size on the development and moulting rates of *Calanus pacificus* and *Pseudocalanus* sp. *Mar. Biol. 56*, 135–146.

Vidal, J. & Smith, S. L. (1986). Biomass, growth, and development of populations of herbivorous zooplankton in the southeastern Bering Sea during spring. *Deep-Sea Res. 33*, 523–556.

Wiborg, K. F. 1955: Investigations on zooplankton in coastal and offshore waters of western and northwestern Norway. With special reference to the copepods. *Fisk.dir. Skr. Ser. Havunders. 11(1)*, 1–246.